Reference: *Biol. Bull.*, **154**: 157–175. (February, 1978)

DEVELOPMENT OF THE EOLID NUDIBRANCH *CUTHONA NANA* (ALDER AND HANCOCK, 1842), AND ITS RELATIONSHIP WITH A HYDROID AND HERMIT CRAB

BRIAN R. RIVEST [1]

Department of Zoology, University of New Hampshire, Durham, New Hampshire 03824

Two aspects of the biology of the eolid nudibranch *Cuthona nana* (Alder and Hancock, 1842) are examined here. The development of *C. nana* was studied because poecilogony (different developmental patterns within a species) was suspected. The distribution and behavior of *C. nana* was investigated because of the nudibranch's specialization on a sedentary prey species which is effectively mobile due to its commensal relationship with hermit crabs.

In 1971 cultured egg masses of *Cuthona nana* developed into actively swimming, planktotrophic veligers; whereas egg masses cultured in 1973 produced lecithotrophic, nonswimming veligers that metamorphosed within a day or two of hatching (Harris, Wright, and Rivest, 1975). Poecilogony may occur in some opisthobranchs (Berrill, 1931; Rasmussen, 1944; Franz, 1970, 1971), but this phenomenon is rare among marine benthic invertebrates and needs to be investigated further.

In the study reported here, egg masses cultured initially in the presence of the adult's food, *Hydractinia echinata* Fleming, 1828, developed only in the nonpelagic lecithotrophic mode. In an attempt to induce alternate modes of development, temperature, adult nutrition and exposure to *H. echinata* were manipulated on different egg masses and embryogenesis and metamorphosis were followed. Field data are compared with laboratory observations.

The ecology of *Cuthona nana* involves a species-specific predator-prey association with the colonial hydroid, *Hydractinia echinata*, commonly found on gastropod shells occupied by pagurid crabs (Fig. 1). *Hydractinia echinata* is a dioecious hydroid consisting of a basal mat from which arise gastrozooids, gonozooids, and defensive dactylozooids (Hyman, 1940). The motile nature of hermit crabs gives the hydroid's substrate a mobility that presents potential settlement problems for the veligers or newly metamorphosed juveniles of *C. nana*, and possible prey-locating difficulty for adult nudibranchs. Information from the literature, laboratory and field observations, and experiments reveals how the behavior and life histories of the hydroid, nudibranch and hermit crab are inter-related.

Materials and Methods

Specimens of *Cuthona nana*, their egg masses, and hermit crabs in mollusc shells bearing *Hydractinia echinata* were collected by scuba diving in Gosport Harbor at the Isles of Shoals (43° 59′ N; 70° 37′ W), *ca.* 10 km off the New Hampshire coast. Most of the collecting was done at the depth of 3–12 m in Haley's Cove, an

[1] Present address: Department of Zoology, University of Washington, Seattle, Washington 98195.

area within the harbor that had the highest concentrations of hermit crabs with *H. echinata* colonies. Monthly field observations and collections were made from January, 1974, to July, 1975, excluding June through August, 1974. The hermit crabs, hydroid colonies, and nudibranchs were maintained at 11–13° C in a recirculating seawater system. Within two days of their collection, the colonies of *H. echinata* were examined under a dissecting microscope and the numbers and lengths of *C. nana* individuals found on each shell were recorded. The ciliated epithelium of the nudibranchs gave them a slight iridesence in contrast to the hydroid, so that even very small nudibranchs (<0.5 mm) could be seen among the polyps.

Egg masses laid in the laboratory were isolated in small dishes containing 50 ml of sea water and incubated at 11–13° C. The sea water used for culturing was collected in Gosport Harbor and filtered through a 0.45 μm Millipore filter. The culture water was initially changed daily, but in later experiments it was changed every two or three days with no effect on development. At intervals of six to twenty-four hours, the egg masses were temporarily transferred in drops of sea water to microscope slides and observed under a compound microscope using transmitted or reflected illumination. Egg masses collected in the field were cultured at the temperature at which they were collected, which ranged from 4–13° C.

The normal mode of development for *Cuthona nana* eggs cultured at 11–13° C was determined initially, then the effect of variations in temperature, adult nutrition, and the presence of *H. echinata* was tested. Specimens of *C. nana* and *H. echinata* colonies were kept in dishes of aerated sea water at 4, 8, or 16° C. Deposited egg masses were isolated as above and incubated at the same three temperatures. At 16° C, successful development was obtained only when the water was changed at least twice daily. Egg masses from starved adults were isolated at 11–13° C and their development followed.

Other specimens of *Cuthona nana* were kept in compartmentalized trays with flowing sea water. Shells covered with *H. echinata* were included with some specimens of *C. nana*. The growth of individual nudibranchs could thus be followed, the availability of food controlled, and the number of egg masses laid by particular individuals monitored.

Although the behavior and distribution of the early postlarval stage of *C. nana* could not be directly studied in the field, the distribution of juveniles on *H. echinata* colonies was noted monthly and two field experiments were conducted to test for the presence of planktonic *C. nana* veligers. In the first, a float was anchored 3 m off the bottom of Haley's Cove in 8 m of water on February 24, 1974. Pairs of *H. echinata*-covered shells were suspended at 1, 2, and 3 m off the bottom to determine if *C. nana* veligers, should they be capable of swimming, would settle directly on an *H. echinata* colony. These hydroid colonies had been collected approximately two weeks earlier, and had been examined under the dissecting microscope to remove all specimens of *C. nana*. The second experiment involved anchoring a 1 × 1 × 0.5 m open-bottomed cage covered with 0.25 inch nylon mesh on the sand near the float. The hermit crabs initially enclosed by the cage were removed before nine hermit crabs bearing *H. echinata*-covered shells were placed inside. These colonies had also been cleaned of *C. nana*. It was hypothesized that planktonic *C. nana* veligers might settle near *H. echinata* colonies before metamorphosing

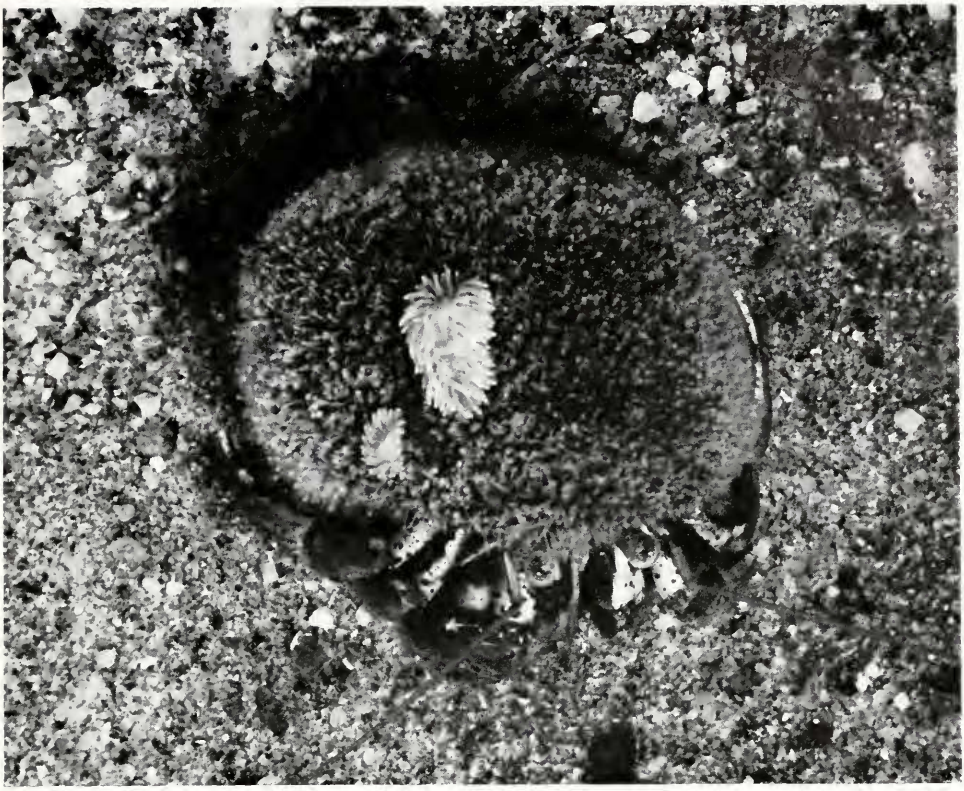

FIGURE 1. Two specimens of the eolid nudibranch *Cuthona nana* feeding on the colonial hydroid *Hydractinia echinata* covering a gastropod shell occupied by the hermit crab *Pagurus acadianus*. The larger nudibranch is about 14 mm in length.

and climbing onto the hydroid. The shells suspended from the float or confined inside the cage were changed at two week intervals until May 29, 1974. Each time, the hydroid colonies were examined for nudibranchs immediately upon return to the laboratory, and again one and two weeks later.

RESULTS

Development

Egg mass. Cuthona nana is reproductively typical of opisthobranchs in that it is a reciprocally copulating hermaphrodite that deposits eggs within a gelatinous stroma. The spawn of *C. nana* has been described and illustrated by Harris *et al.* (1975). The largest egg masses collected in the field or laid in the laboratory were 10 mm in diameter and contained about 1500 eggs. However, most egg masses observed were considerably smaller, averaging 450 eggs. Nudibranchs raised in the laboratory from immaturity to death laid up to 16 egg masses. The first and last few egg masses laid were smaller than average, but most contained 300–600 eggs. Individuals separated after copulation laid up to six egg masses before a substantial number of unfertilized eggs were produced.

TABLE I

Normal table of development for Cuthona nana *eggs incubated at 11–13°C.*

12 hours	First division	6–10 days	Cilia and shell develop
16 hours	Second division	15 days	Mantle withdrawn half-way
20 hours	Third division	16 days	Propodium first appears
36 hours	Morula	18–21 days	Hatching
3–5 days	Gastrulation	20–23 days	Metamorphosis

Development to hatching. Early development in *Cuthona nana* is similar to that described for other opisthobranchs (Casteel, 1904; Pelseneer, 1911; Thompson, 1958). Table I gives normal development time for eggs cultured at 11–13° C. At oviposition, the white eggs within their individual ovate capsules average 160 μm in diameter. Spiral cleavage produces a stereoblastula whose vegetal side begins to flatten at the end of the second day of development. Gastrulation results in a cup-shaped gastrula, with the ventral blastopore becoming asymmetrical before closing during the fifth day. Typically, the polar bodies adhere to the animal pole through gastrulation.

By the end of the sixth day a shell cap covers the posterior end of the embryo (Fig. 2a). The shell increases in size as the shell gland (now the mantle fold) spreads anteriorly. Two anal cells of disputed function (see Bonar and Hadfield, 1974) appear in front of the mantle fold on the right, ventro–lateral surface of the embryo, while anteriorly the velar lobes and foot are enlarging. The locomotor cilia elongate and rock the embryo within the egg capsule. The rate of shell formation exceeds the speed at which the mantle fold migrates anteriorly, so that a lumen (the perivisceral cavity) develops in the posterior end of the shell (Fig. 2b–c). The visceral mass is compact and opaque, occluding the anterior opening of the developing shell. The retractor muscle is visible within the perivisceral cavity, but shows no signs of contracting during shell formation. A group of cells surround its origin just dorsal and to the left of the shell apex. The anal cells remain visible for a time in front of the mantle fold but disappear before the shell becomes complete on the tenth day. Torsion in *C. nana* does not involve a 180° twist of the cephalo-pedal elements with respect to the shell; these parts differentiate in their post-torsional positions. The movement of the anal cells may be the only ontogenetic evidence of torsion (Thompson, 1962).

During shell growth the foot elongates ventrally and becomes heavily ciliated mid-ventrally and at the tip, but not laterally. Its dorsal surface has an operculum by the ninth day and several long, stiff compound flagella protrude from the tip. At this time, a ciliated subvelar ridge begins to develop. The visceral organs grow posteriorly into the perivisceral cavity, eventually filling the entire posterior end of the shell except for the dorsal mantle cavity. Due to the yolk content and opacity, it is difficult to discern individual organs.

When secretion of the larval shell is complete, the mantle fold at the shell aperture becomes thinner and less dense. By the eleventh day, it begins to withdraw posteriorly along the inner surface of the shell. The degree to which the velar lobes can be retracted into the mantle cavity depends on the position of the withdrawing mantle fold. Initially, the velum cannot be accommodated by the

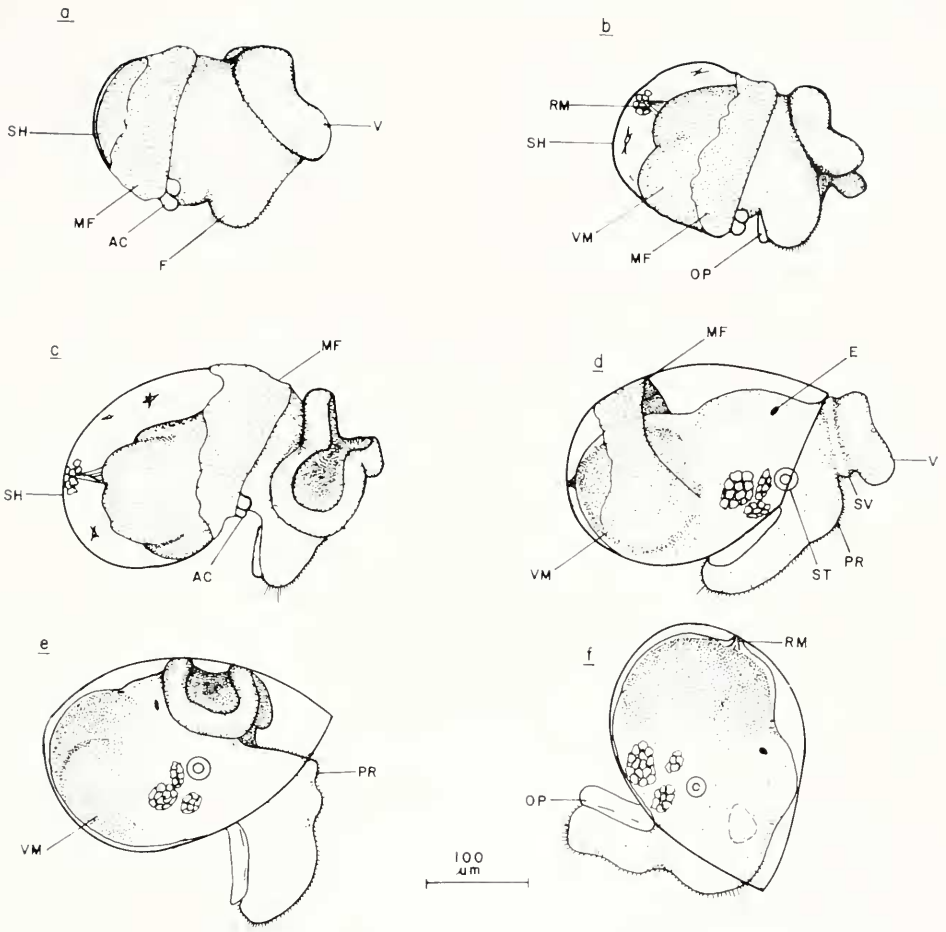

FIGURE 2. Late larval development and early metamorphosis in *Cuthona nana:* a–c) veliger with developing shell; d) veliger with complete shell and mantle withdrawn back along inside of the shell; e) late veliger retracted into the shell at the stage of development at hatching; and f) early metamorphosis after loss of the velum. AC indicates the anal cells; E, the eye; F, the metapodium; MF, the mantle fold; OP, the operculum; PR, the propodium; RM, the retractor muscle; SH, the shell; ST, the statocyst; SV, the subvelar ridge; V, the velum; and VM, the visceral mass. Velar locomotor cilia not shown.

mantle cavity, and only when the mantle has regressed three quarters of the way to the apex of the shell (Fig. 2d) can the velar lobes be entirely withdrawn. Normally, the foot is never fully retracted with the operculum closing the shell opening. Chemical irritants such as alcohol cause the veliger to retract beyond the normal restrictions of the mantle fold or even to draw the foot into the shell, but only at concentrations that kill the larva.

Two red eyespots become visible on the fifteenth day. A day later, the propodium begins to form, just ventral to the mouth (Fig. 2d). At this stage the mantle has migrated two-thirds of the way back from the shell aperture. The sub-

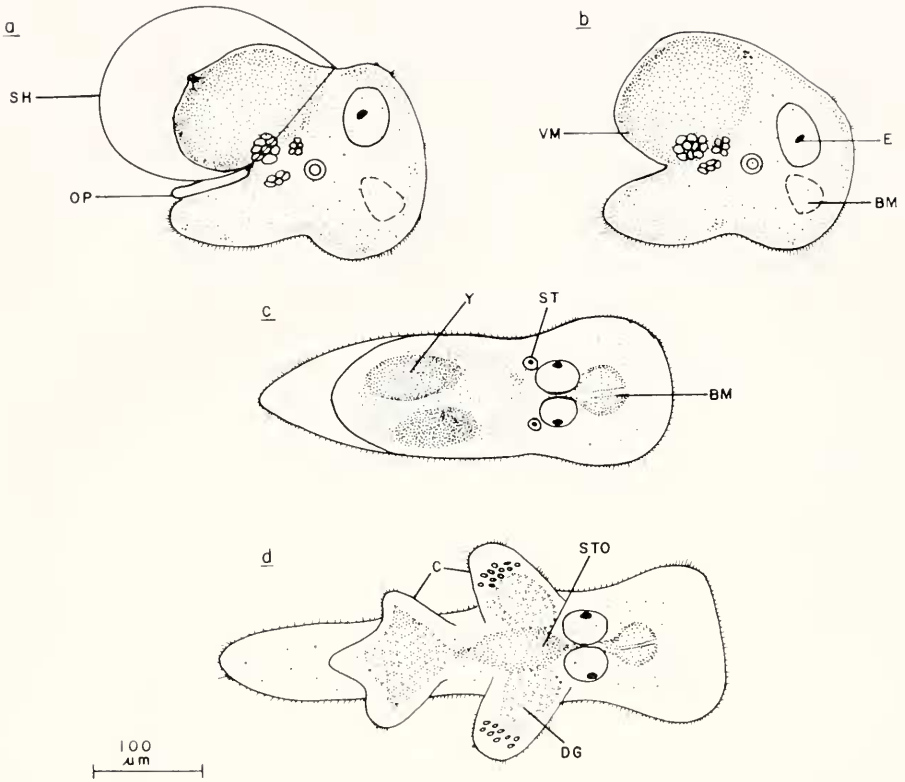

FIGURE 3. Late metamorphosis and early postlarval development in *Cuthona nana:* a) shell loss; b) newly emerged juvenile; c) elongated juvenile; and d) juvenile with four primary cerata. Stages a-c occur in 20–23 days after oviposition at 11–12° C. Growth to stage d occurs in another 2–3 weeks in the presence of abundant food. BM indicates the buccal mass; C, two cerata; DG, the digestive gland; E, the eye; OP, the operculum; SH, the shell; STO, the stomach; VM, the visceral mass; and Y, yolk concentrations in the visceral mass.

velar ridge is well-developed and heavily ciliated. By the eighteenth day the mantle has reached the shell apex, and fuses with the epithelial layer covering the visceral mass. The veliger is attached to the shell only around the origin of the larval retractor muscle, and possibly ventrally. In another day the propodium is fully developed (Fig. 2e), and muscular activity in the foot is evident. The velar locomotor cilia continue to beat almost continuously, but the veligers move about very little within the capsules. The visceral organs are still densely packed with yolk, while the foot and velum have become progressively less opaque.

Hatching. The rate of development varies slightly among siblings, although there is no noticeable relationship between position in the egg mass and developmental rate. The hatching of larvae from an egg mass is usually spread over several days. At 11–13° C, a few veligers typically begin escaping from their capsules late on the eighteenth day after oviposition. Cracks develop and radiate throughout the egg capsule causing its collapse. Although at this time the uniseriate

radula possesses two distinct teeth, it is not used to rupture the capsule wall. Furthermore, the physical activity of the veligers does not change markedly prior to hatching. It is thus unclear what causes the breakdown of the capsules. Also, hatching from the capsules does not depend on the integrity of the egg mass. Usually the gelatinous stroma of the egg mass deteriorates before the eggs hatch, but when incubated in still, filtered sea water this outer covering often remains intact. The process of hatching is identical in either situation.

The behavior of newly hatched veligers depends on their relative stage of development. Veligers may hatch prior to the complete development of the propodium. These larvae initially lay on their sides with the velum extended and velar cilia beating. Although the cilia may gently rock the veliger, or even lift the anterior end off the substratum so that it faces upward, a veliger was never seen to swim up into the water. When the propodium is more fully developed, the veligers roll over and crawl slowly about, with the velum only partially extended. Veligers that hatch with a well-developed propodium immediately adhere to the bottom and begin crawling. Movement may continue for up to two days, but activity progressively decreases.

Metamorphosis. Within a day or two of hatching, metamorphosis begins. The veligers cease crawling and remain in a semi-contracted state, with the shell held nearly vertically and the head just inside the shell aperture. The first noticeable morphological change is the loss of the velar lobes. The beat of the locomotory cilia becomes increasingly erratic. Cells bearing these cilia are cast off from the velum. In individuals still held within the egg mass stroma, these cells do not accumulate but appear to be ingested, as are homologous cells shed during metamorphosis in *Phestilla sibogae* (Bonar and Hadfield, 1974). The rest of the velar lobe is resorbed during the next several hours, until only a swelling remains protruding slightly from the dorsum.

During this period, loss of contact between the larval body and shell continues ventrally until only the retractor muscle attachment remains (Fig. 2f). The operculum is still attached to the dorsal surface of the metapodium but becomes progressively detached distally, allowing increased flexibility of the foot. Activity of the retractor muscle diminishes. By the time the velar lobes are resorbed, mechanical and nonlethal chemical stimuli do not elicit further withdrawal of the larva into the shell. Should the larva become dislodged from the substrate, the pedal cilia slowly spin it about until a foothold is regained.

Shell loss begins when a strong, continuous contraction of the retractor muscle breaks its connection with the shell. This occurs only if the foot is firmly attached to the substratum. For several hours after the connection is broken, the remnant of the origin of the retractor muscle may be visible as a small lump of cells or thickening in the epidermal layer. In some metamorphosing larvae this lump is not seen, possibly due to a more contracted state of the retractor muscle after it detaches from the shell. With the retractor muscle attachment severed, the larvae are free to crawl out of the shell (Fig. 3a), a process that may take five to eight hours in still water. Loss of the shell may be greatly accelerated by water currents, because the visceral mass is compact and equal to or just smaller in diameter than the shell aperture. The operculum may adhere to the shell when it is cast off or is lost separately.

The visceral mass of the young shell-less juvenile initially appears as a distinct hump (Fig. 3b). Within a day it fuses with the cephalo-pedal elements, thereby flattening the nudibranch dorso-ventrally. Elongation of the body continues until the juvenile measures about 0.32 mm in length (Fig. 3c). The developing buccal mass possesses three to four teeth in the uniseriate radula and a pair of weak jaws. The body is generally a translucent white color, with the red eyes clearly visible near the cerebral ganglia. The visceral mass is cream-white, indicating that yolk still remains. Cilia densely cover the ventral epithelium, but are sparse on the dorsum.

The effect of different temperatures on development. The development of eggs laid and maintained at 4, 8, or 16° C differed from those kept at 11–13° C only in the length of time until metamorphosis. Egg size did not vary with temperature. Metamorphosis occurred within 50–55 days at 4° C, 34–36 days at 8° C, and 16–17 days at 16° C. *Cuthona nana* may not tolerate temperatures much above 16° C, for specimens maintained at that temperature suffered a high rate of mortality. Eight adults placed with food at 16° C died within 10 days. Only 5–30% of the eggs from spawn laid at 16° C or transferred to that temperature from 11–13° C immediately following oviposition developed normally through metamorphosis. In contrast, nearly all of the eggs laid and maintained at 11–13° C reached metamorphosis. Nine egg masses collected in the field and incubated at the temperature at which they were collected (4–13° C) developed and metamorphosed normally, with their rates of development varying according to the temperature, and they are identical with those observed for eggs raised in the lab at similar temperatures.

The effect of adult nutrition and the presence of Hydractinia echinata *on larval development.* Hatching and the events of metamorphosis proceeded sequentially, unaffected by the presence of *H. echinata* during any stage of development. The development of embryos in egg masses incubated in a dish with *H. echinata* and those exposed to the hydroid only before or after hatching did not differ from the development of those egg masses kept isolated. The integrity of the spawn mass had no effect. The development and metamorphosis of larvae from egg masses that had broken down, exposing the capsules directly to the water, was similar to those in egg masses that remained intact.

Adult specimens of *C. nana* kept without food in Millipore-filtered sea water continued to lay egg masses for up to ten days. The size and activity of the adults progressively diminished during that time, but some starved individuals survived for 17 days. They laid several egg masses in the first few days of isolation, but the frequency of oviposition and the number of eggs per spawn decreased with time. Mean egg diameter did not vary, and the rate and events of larval development and metamorphosis proceeded normally in the presence or absence of *H. echinata.*

Postlarval development to the adult stage. In the absence of *H. echinata,* the newly metamorphosed juveniles crawl about constantly. They are negatively geotactic and positively phototactic, crawling up the sides of the dishes and toward unidirectional illumination or to the apex of rocks or shell fragments placed in their dishes. When *H. echinata* is added, movement is directed toward the hydroid. However, in the absence of food, activity decreases. Starved postlarvae become motionless within two weeks of metamorphosis, but movement increases rapidly when *H. echinata* or water exposed to the hydroid is added. Postlarvae survived

for five to six weeks without food at 11–13° C and ten weeks at 4° C, and were then still capable of feeding and growing if *H. echinata* was made available. Postlarvae from four egg masses laid by starved adults at 11–13° C survived up to six weeks without food. As the juveniles are starved, the visceral mass becomes less intensely colored. Teeth are added to the radula until there are five to eight, but no more are formed unless feeding begins.

Cuthona nana is attracted to *H. echinata* almost immediately after metamorphosis, but feeding is initially very slow if it occurs at all. In animals that crawl onto *H. echinata* shortly after metamorphosis, the orange color of the hydroid does not appear in the digestive gland of the nudibranchs for two or three days. However, juveniles that are not given food until four or five days following shell loss begin feeding immediately and color appears in the digestive gland within 24 hours. Development of the postlarval buccal or digestive structures necessary for feeding may therefore continue for several days following shell loss.

Cuthona nana will readily feed on any part of *H. echinata* colonies, as well as released eggs, planula larvae, or metamorphosing planulae. Young nudibranchs are sometimes much smaller than the hydranth they are feeding on, especially the gastrozooids. These polyps are very distensible and may reach a length of 5 mm or more and an oral disc diameter of more than 0.75 mm. Many of the prey items ingested by the gastrozooids are much larger than the newly metamorphosed nudibranchs, but recently collected and presumably well-fed colonies of *H. echinata* do not attempt to ingest the small eolids. On such colonies maintained in still water, postlarvae are often seen on the manubrium of gastrozooids. Small nudibranchs sometimes elicit a defensive response by *H. echinata;* the tentacles of several nearby polyps are brought down on top of them, but the hydroid's nematocysts apparently do no harm. In contrast, hydroid colonies starved for several weeks will eat recently metamorphosed *C. nana* juveniles. The nudibranchs are not killed before ingestion, and will survive if immediately removed from the gastrocoel of the hydranth. Those removed an hour or more later are dead and partly digested.

Table II summarizes post-metamorphic growth in *C. nana.* Growth is initially slow, even with an abundance of *H. echinata.* Dorsal enlargements, indicating the rudiments of the first pair of cerata, do not appear for two weeks after metamorphosis. The second pair of ceratal buds develop posterior to the first pair within another five days (Fig. 3d). New cerata develop at an increasingly rapid rate, with their pattern of appearance like that described for *Cuthona adyarensis* by Rao (1961). The uniseriate radula also grows in size, with new teeth being distinctly larger than the first five or six. Eventually *C. nana* adults may attain a length of 28 mm with 250 cerata and 27 radular teeth, but nudibranchs measuring 17–22 mm with 23–24 radular teeth are more common.

Development and growth varies substantially in individuals from the same egg mass, so that some mature several weeks before others. The white ovotestis first becomes visible through the body wall when the nudibranchs are 8–10 mm long. Anterior acini of the ovotestis develop first, and maturation proceeds posteriorly. Nudibranchs smaller than 10 mm have never been seen to copulate, and they are usually longer than 12 mm before they lay eggs. In the laboratory, specimens of *C. nana* raised on healthy *H. echinata* on a gastropod shell remained on that colony until they were at least 10 mm long, regardless of the presence or absence of a

TABLE II

Postlarval growth in Cuthona nana *in the presence of abundant* Hydractinia echinata *at 11–13°C.*

Time from metamorphosis	Length in mm	Characteristics
2 weeks	0.5	Eight to ten radular teeth; first pair of cerata
3 weeks	0.75	Eleven to twelve radular teeth; third pair of cerata; rhinophore primordia
4–5 weeks	1.0	Fifteen radular teeth; fourteen cerata; first heart beat; oral tentacles appear
6–7 weeks	4.0	Thirty to thirty-five cerata
9–10 weeks	8.0	Nineteen to twenty-four radular teeth
11 weeks	12.0	Shortest time observed for an individual to mature and lay an egg mass

hermit crab in the shell. At this time, if alone, *C. nana* leaves the hydroid colony in search of a mate. When a nudibranch measuring only 10–12 mm mates for the first time, it usually resumes feeding before laying egg masses.

Harris *et al.* (1975) reported that *Cuthona nana* adults do not lay egg masses on *H. echinata* colonies. They noted that since the nudibranchs do not die after laying eggs, they probably find new hydroid colonies. Subsequent laboratory observations were made on *C. nana* confined with hermit crabs bearing *H. echinata*-colonized shells. The nudibranchs invariably left the hydroid to lay egg masses and consistently returned to the colonies to resume feeding. The hermit crabs often remained motionless long enough for the nudibranch to find and crawl onto the hydroid. This pattern of leaving the *H. echinata* to deposit spawn, and then returning, continued until the nudibranchs died. At 11–13° C, adult specimens of *C. nana* survived in this fashion for six to eight weeks, while those kept at 4° C lived for over three months.

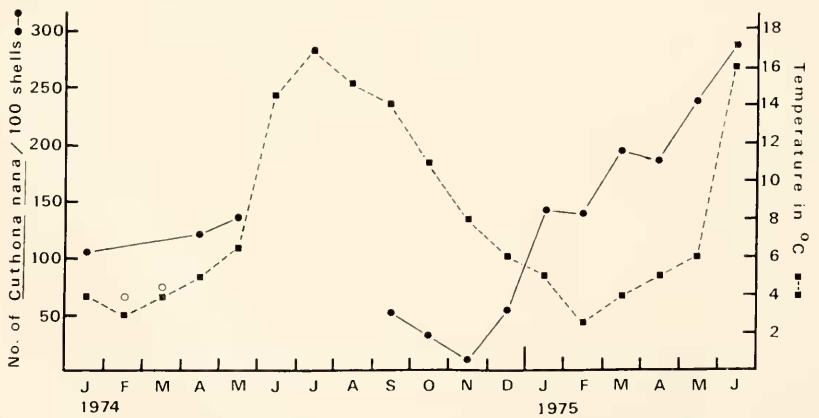

FIGURE 4. Number of *Cuthona nana* per 100 *Hydractinia echinata* colonies and surface water temperatures from January, 1974, to June 1975. Open circles refer to collections outside of Haley's Cove. No collections were made in June, July and August, 1974. See text for details.

Two generations of *Cuthona nana* were raised in the laboratory at 11–13° C. The nudibranchs survived well in the recirculating seawater systems where the salinity varied from 30 to 38‰. The shortest life cycle observed took 14 weeks from egg to egg.

Ecology

Cuthona nana was found to be more abundant in Gosport Harbor than previously reported (Harris *et al.,* 1975). Both juvenile and adult individuals were most common from January through June and least abundant in September through December (Table III). The number of *C. nana* observed in February and March, 1974, were considerably below that seen in those months during 1975. Foul weather in February and March, 1974, forced collection outside of Haley's Cove, the area where the density of pagurid crabs with *Hydractinia echinata* colonies was highest in Gosport Harbor. Laboratory studies have shown that the growth rate of *C. nana* at water temperatures observed during these months (3.5–4.5° C) is extremely slow. Therefore, the number of nudibranchs found in April and May, 1974, when the temperature reached only 6.5° C, indicates that nudibranch densities within Haley's Cove during the previous two months were much higher than in the collections outside Haley's Cove. Nudibranch numbers fluctuated asynchronously with temperature (Fig. 4). The population of *C. nana* was growing in size during the coldest months and decreased sometime during the summer. The average size of the nudibranchs collected varied little, for the number of adults and juveniles varied synchronously (Table III). Egg masses were seen in the field during every month of this study except for September and November, 1974. In October, 1974, only one egg mass was found, and only two were found in December. Reflecting the greater number of adults, egg masses were more abundant during the spring months with up to eight seen during a forty-minute dive.

Data on the distribution of *C. nana* less than 5 mm in length are included in Table III to show monthly differences in the numbers of juveniles and to evaluate seasonal fluctuations in reproduction and recruitment. Since young nudibranchs normally do not leave an *H. echinata* colony until they are about 8–10 mm in length, the 5 mm length was considered a conservative upper size limit for examining the distribution of nonreproductive juveniles. Such juveniles were likely to be found on the first hydroid colony they had occupied.

The numbers of *C. nana* juveniles fluctuated from a spring high of 94 in May, 1974, down to a fall low of 7 in November, 1974, and up to 242 per 100 hydroid colonies in June, 1975 (Table III). These juveniles were not evenly distributed over the population of *H. echinata* colonies. In the months when most abundant, young nudibranchs outnumbered the hydroid colonies collected, yet they were found on only 48–57% of them. Thus, if one small nudibranch was present on an *H. echinata* colony, chances were good that there were more. Four or five juveniles per colony were not uncommon, and much higher numbers were occasionally found. In May, 1974, one colony collected possessed 17 juveniles less than 3.5 mm long. A colony examined in June of 1975 carried 29 *C. nana* juveniles. During the fall months when *C. nana* was least abundant, *H. echinata* colonies with two or more young nudibranchs were still more frequently encountered than those with just one.

Cuthona nana juveniles were also not randomly distributed over the *H. echinata*

TABLE III

Data on Cuthona nana *from monthly collections of* Hydractinia echinata-*covered hermit crab shells from Gosport Harbor.*

Month	Number of *C. nana* per 100 shells*		Number of *C. nana* by size classes			Average size of *C. nana* in mm	Number of hermit crab shells examined	Percentage of shells with *C. nana*		Average number of *C. nana* <5 mm per infested shell
	<5 mm	Total	<5	5–10	>10 mm			<5 mm	Total	
Jan. 1974	90	107	26	2	3	3.1	29	41	59	2.2
Feb.**	24	67	5	8	1	6.1	21	14	43	1.6
Mar.**	9	56	2	6	4	8.5	22	9	36	1.0
Apr.	89	121	34	8	4	3.5	38	38	42	2.8
May	94	138	76	19	17	4.5	81	44	59	2.1
Sept.	46	51	31	4	0	2.6	68	24	25	1.9
Oct.	19	31	13	6	2	4.0	67	10	25	1.8
Nov.	7	11	4	1	1	4.4	55	7	11	1.0
Dec.	50	53	29	1	1	1.8	58	31	34	1.6
Jan. 1975	128	144	32	1	3	2.9	25	48	56	2.7
Feb.	123	139	54	4	3	2.9	44	52	61	2.4
Mar.	152	193	70	12	7	3.7	46	54	72	2.8
Apr.	143	188	80	18	7	3.4	56	57	71	2.5
May	180	238	88	15	14	2.8	49	55	65	2.7
June	242	285	138	10	15	2.4	57	53	70	4.6
										$\bar{X} = 2.7$

* These columns were obtained by adjusting the number of *C. nana* found in the monthly samples to 100 hermit crab shells so that population size fluctuations would be more visible.

** Collections during these months were made outside of Haley's Cove, and the number of *C. nana* found was lower than expected for Haley's Cove. See text for details.

colonies. The observed distribution of nudibranchs over the hydroid colonies collected each month was compared with a random distribution using a chi-square analysis. The differences were significant at the 0.05 level for the Haley's Cove samples for all months except October, November, and December, 1974. Thus, during the months when most abundant, the juveniles were nonrandomly distributed over the H. *echinata* colonies.

Two observations suggest that recruitment of *C. nana* on hydroid colonies is from benthic juveniles rather that pelagic veligers. First, no juveniles were found on either the caged pagurids or the suspended *H. echinata* colonies that were placed in the field during a period with high *C. nana* egg production and a growing population (February through May, 1974). In the laboratory, starved colonies of *H. echinata* had consumed veligers and postlarvae of *C. nana*. Therefore, the hydroid colonies recovered from the float and cage were tested to determine if the experimental manipulations had starved them to a point where they might have eaten any *C. nana* veligers or postlarvae they had contacted. Veligers and juvenile nudibranchs were not preyed upon when placed on the gastrozooids of experimental colonies shortly after being brought back from the field.

Secondly, *C. nana* juveniles smaller than 3 mm in length were found predominantly on the ventral half of the hydroid colonies collected. The gastrozooids of *H. echinata* are more numerous and longer around the ventral periphery of the

colony. These polyps sweep over the surface of the substrate as the hermit crab moves about. In the laboratory, *H. echinata* colonies swept over the bottom of dishes containing *C. nana* postlarvae picked up many of the small nudibranchs by a mechanism that probably involves the hydroid's nematocysts. These collected nudibranchs then reoriented and began feeding on the hydranths. By the time they had grown to a length of 5 mm, they may have moved half way around the colony. Since the location of nudibranchs less than 3 mm in length is close to the site of first contact with the colony, the ventral position of the smallest *C. nana* individuals on the collected *H. echinata* colonies supports the hypothesis that the nudibranch reaches the hydroid by being swept up from the bottom and not by settling onto the hydroid from the plankton.

In the field, most individuals of *C. nana* were observed on *H. echinata* colonies, but during the late spring months adult nudibranchs were often found crawling over the sand, rubble, or loose pieces of algae. Occasionally groups of two to four were seen, either copulating or depositing egg masses, but most were isolated individuals. Five adult nudibranchs found singly on the bottom or on a hydroid colony were returned to the laboratory and maintained in isolation. In every case, fertile egg masses were subsequently laid, indicating that the adults had copulated previously.

In late April and May, 1974, large specimens of *C. nana* were discovered in the cage. During each of four two-week periods, four to six nudibranchs with average lengths of 16 mm had crawled onto the hydroid colonies, and several more were seen in and around the cage. The presence of adults of *C. nana* on the caged *H. echinata* demonstrates the nudibranch's mobility and capacity for finding new colonies.

The pagurid population in Gosport Harbor consisted of *Pagurus acadianus* Benedict, 1901, and *P. arcuatus* Squires, 1964. Both were abundant down to a depth of twelve meters. *Pagurus acadianus* was found more commonly on the cleaner sand and *P. arcuatus* in the siltier, more cobble-strewn areas, but there was considerable intermixing. Observations during numerous dives indicated that the distribution of these hermit crabs changed continuously, such that denser concentrations were found in different areas of Haley's Cove on successive dive dates. Grant (1963) also found that populations of *P. acadianus* in the shallow subtidal were transient in nature, indicating a high degree of mobility. The feeding behavior of this pagurid has not been described, but it appears to be similar to that of the omnivorous European species, *P. bernhardus* (Orton, 1927; Gerlach, Ekstrøm and Eckardt, 1976). Food of *P. acadianus* consists partly of moribund invertebrates and pieces of algae, but predominantly of detrital material and small organisms captured by using the chelae to shovel sediment into the mouth parts where it is sifted. The hermit crabs remained stationary much of the time, sifting sediment or actively fanning the water with the maxillipeds and maxillae, possibly filter-feeding as in *P. bernhardus* (Gerlach *et al.*, 1976). *Pagurus acadianus* broods its eggs on abdominal pleopods until the zoeal stage. Females were seen in March, 1974, to release the zoeae by protruding three-fourths of the way out of their shells and waving their egg-laden pleopods. In cases where the shell aperture was lined by *H. echinata,* some zoeae were caught and eaten by the gastrozooids. Of all the hermit crabs collected bearing shells colonized by *H. echinata,* 98% were *Pagurus acadianus.* Like the European *P. bernhardus* (Jensen, 1970), *P. acadianus* prefers

shells covered with the hydroid over clean shells (Grant and Ulmer, 1974). In contrast, *P. arcuatus* preferentially selects naked shells (Grant and Ulmer, 1974). (*Pagurus pubescens* in Grant and Pontier, 1973, and Grant and Ulmer, 1974, was actually *P. arcuatus;* personal communication from W. Grant, 1975.) Whereas empty, clean gastropod shells were commonly seen in Gosport Harbor during the present study, unoccupied *H. echinata*-covered shells were rare.

The feeding of juvenile nudibranchs had little noticeable effect on the hydroid colonies; the regeneration rate of the hydranths approximated the predation rate. Adult nudibranchs, however, cleared patches among the hydranths, leaving only the basal mat. In such cases, the first polyps eaten were often regenerating while the nudibranch was still enlarging the patch.

Discussion

The pattern of development of *Cuthona nana* eggs remained constant over a variety of conditions during this study. Incubation of egg masses collected in the field throughout the year and those laid in the laboratory under various conditions of temperature and adult nutrition yielded veligers which invariably metamorphosed without a pelagic stage. Developmental rate varied inversely with temperature. The times to hatching obtained at 4, 8, 11–13, and 16° C fall close to the regression line of Spight (1975, Fig. 1) for prehatching period *versus* temperature for other opisthobranchs. These results further support his thesis that time to hatching can be estimated with reasonable accuracy from taxonomic affinity and temperature alone.

The presence or absence of *Hydractinia echinata* had no noticeable effect on the rate or sequence of events in the development of *C. nana*. Egg size and subsequent development were unaltered by differences in adult nutrition; starved animals simply laid fewer eggs. In contrast to *Mytilus edulis* (Bayne, 1972; Bayne, Gabbott, and Widdows, 1975), there was no increase in abnormal development in eggs from starved adults. Furthermore, starved postlarvae from starved adults developed as fast and survived as long (four to six weeks at 11–13° C) as starved postlarvae produced by well-fed adults. *Hydactinia echinata* apparently plays no role in inducing metamorphosis in *C. nana,* as *Electra pilosa* does for *Aldaria proxima* (Thompson, 1958).

Two schemes that categorize opisthobranch development have been presented in the literature. Thompson (1967) formed three categories distinguishing opisthobranchs by feeding type and place of metamorphosis. His development-types 1, 2, and 3 refer to species with pelagic planktotrophic, pelagic lecithotrophic and nonpelagic lecithotrophic ("direct") development, respectively. *Cuthona nana* falls between development-types 2 and 3 in that it does not possess a pelagic lecithotrophic larva, nor does it hatch out of the capsule at a post-veliger benthic stage. Because of the ecological significance of its nonpelagic development, it should be classified as having development-type 3. In this category Thompson (1967) included *Cuthona pustulata,* which like *C. nana* hatches out of the capsule as a veliger, but remains within the stroma of the egg mass until metamorphosis (Roginskaya, 1962).

Tardy (1970) presented a classification scheme for the Nudibranchia that primarily segregated them on the basis of protoconch type, which he felt represented

basic ontogenetic differences such as different origins of the adult dorsal epidermis. Species with a spiral protoconch were categorized as having type 1 development, while type 2 referred to those species possessing an inflated protoconch. There are at least two exceptions to Tardy's scheme. First, Bonar and Hadfield (1974) and Bonar (1976) have reported that the dorsal epidermis of *Phestilla sibogae* was derived from the lateral surfaces of the larval foot and not from the floor of the mantle cavity as thought by Tardy for type 2 nudibranchs. Secondly, whereas Tardy felt that all nudibranchs with inflated protoconchs underwent torsion after the shell was complete, in *Cuthona nana* structures develop in their post-torsional positions. Additional studies are needed on the origin of the adult dorsal epidermis and differences in the expression of torsion within the Opisthobranchia.

The field data support the laboratory observations of nonpelagic development in *Cuthona nana*. A pelagic veliger might have settled on the experimental colonies suspended in the water column or enclosed by the cage, but this was not observed. Table III shows that from January to June, 1975, juveniles of *C. nana* were found on only about one-half of the hydroid colonies collected, even though the nudibranchs greatly outnumbered the colonies. The uneven nonrandom distribution observed during the late winter and spring months is what would be expected if recruitment to the *C. nana* population was from simultaneous colonization by clustered benthic juveniles, with the distribution of these clusters being determined by the deposition sites of egg masses.

Predatory benthic marine invertebrates that are relatively nonmotile as adults and lack pelagic larval stages are faced with the problems of prey location and of dispersal. From field and laboratory observations, it is concluded that the postlarvae of *Cuthona nana* 'find' an *Hydractinia echinata* colony much the same way as the hydroid's planulae 'find' a clean hermit crab shell. The gonozooids on female hydroid colonies produce large orange-red eggs that are fertilized when released, drop to the bottom and develop within two or three days into a planula with an enlarged anterior end possessing numerous secretory cells (Bunting, 1894; Van de Vyver, 1964, 1967). A healthy colony covering an hermit crab shell may release several hundred eggs in a season. The resulting planulae remain benthic and crawl slowly about in a turbellarian-like fashion, being positively phototactic and somewhat negatively geotactic (Schijfsma, 1935; Cazaux, 1961; Van de Vyver, 1964). The planulae do not actively search for a clean hermit crab shell; it is the hermit crab's activity, either its locomotion or feeding movements, that bring the two in contact (Schijfsma, 1935). The planulae adhere to the shell with the anterior end. A single polyp is initially formed, then a basal mat grows out over the shell as new polyps are added. The gastrozooids develop primarily around the ventral side of the shell, where they capture small invertebrates on the surface of the substrate during the hermit crab's travels and feeding movements (Christensen, 1967; Harris *et al.*, 1975). Postlarvae of *Cuthona nana* also get picked up by these gastrozooids. Just as with the planulae, the positive phototaxis and negative geotaxis of the nudibranchs keep them in the open on the substrate surface. Such positioning increases the chances that the postlarvae will be swept up by an *H. echinata* colony should an hermit crab bring one by.

The mobility of the hermit crabs is likely to be an important factor in the spread of *Cuthona nana* and *Hydractinia echinata*, for neither species has an actively dis-

persing larva. An adult nudibranch feeding on an *H. echinata* colony will be carried across the bottom as the hermit crab wanders, and may be taken tens of meters before it leaves the colony to find a mate or lay eggs. The next hydroid colony it climbs onto will be carried in a direction and distance independent of the previous ones. Large *Pagurus acadianus* in deeper water (below 17 m) have been seen in *Lunatia* or *Buccinum* shells bearing *H. echinata* and *C. nana*. These large crabs are quite noticeable because of their size, but are relatively rare. Their occasional presence in frequently observed areas indicates they probably travel long distances. They are sometimes seen in shallow water where small hydroid-colonized hermit crab shells are more numerous. By visiting different hermit crab concentrations, these large hermit crabs may provide a means for colonizing new areas and a mechanism of genetic communication between physically distant populations of *C. nana*. Other crab species may also be important; *C. nana* was collected on *H. echinata* growing on the legs and ventral side of a *Cancer borealis* in 18 m of water. Hermit crabs also act as colonization vectors for the direct developing *Crepidula convexa* (Hendler and Franz, 1971).

Cuthona nana may also disperse by rafting on pieces of dislodged algae. Wave-dislodged algae occasionally blanket the bottom in shallow areas of Gosport Harbor. Nudibranchs that climb onto the algae or egg masses deposited there could be carried off by storms or current changes. Data from seabed drifters indicate that the local average water speed is from 0.07 km/day (Loder, Anderson, and Shevenell, 1973) to 0.2 km/day (Graham, 1970). Thus at 4° C, juveniles having developed and metamorphosed on a piece of drifting algae could travel 8.75 to 25 km before starving.

The interspecific association between *Pagurus acadianus* and *Hydractinia echinata* is mutually advantageous. The hermit crab's shell provides a suitable substrate for the hydroid, which in turn makes the shell more desirable for *P. acadianus* and less so for *P. arcuatus* (Rees, 1967; Grant and Pontier, 1973; Grant and Ulmer, 1974). *Pagurus acadianus* will even occupy shells smaller than their preferred size range if these shells are colonized by *H. echinata* (Grant and Pontier, 1973). The hydroid can increase the effective size of the shell by growing beyond the lip, so the hermit crab needs to change its shell less frequently (Harris *et al.*, 1975; Jensen, 1975). *Hydractinia echinata* may act as a deterrent to predation on the pagurid crabs. Grant and Pontier (1973) found that *Cancer irroratus* did not feed on *P. acadianus* occupying shells with *H. echinata* colonies. However, during the present study a few starved specimens of *C. borealis* and *Carcinus maenus* did feed on *P. acadianus* in hydroid-covered shells, although most did not.

The hermit crab's mobility may provide a means of escape from overpredation for *Hydractinia echinata*. The hydroid colonies are perennial and once established, may persist for years (Sutherland, 1975; personal observation). *Cuthona nana* preys on the hydroid by eating the polyps, leaving the basal mat intact. When an adult nudibranch leaves an hydroid colony to search for a mate or deposit eggs, the colony will be carried away, descreasing its chances of being preyed upon by that nudibranch again. During the spring and early summer months, when large specimens of *C. nana* were most common, the majority of the hydroid colonies collected possessed patches devoid of polyps due to grazing by *C. nana*, the only significant local predator of *H. echinata*. However, never was a colony collected that had

more than half of its polyps eaten and usually the grazed areas showed signs of regeneration. *Cuthona nana* thus appears to simply crop *H. echinata* colonies and not kill them, with the perennial colonies regenerating lost polyps. Similarly, *Dendronotos iris* feeds on just a few tentacles of *Cerianthus* sp., not killing the anemone which presumably replaces the lost tentacles (Wobber, 1970).

Precuthona peachi (Alder and Hancock, 1847) has been reported to feed on *Hydractinia* growing on hermit crab shells in Europe (Farran, 1903; Swennen, 1961; Christensen, 1977). Several workers (L. Harris, T. Gosliner, T. E. Thompson, G. Brown; personal communications) consider *P. peachi* to be a junior synonym of *Cuthona nana*. Christensen (1977) recently reported that *P. peachi* in Sweden produced actively swimming planktotrophic veligers. These larvae survived unfed for 14 days without metamorphosing in the presence of *Hydractinia*. Christensen reported an egg diameter for *P. peachi* of 100 μm and a development time to hatching of 20–26 days at 7–9° C. This compares with the respective values determined during the present study on *C. nana* of 160 μm and 31–34 days at 8° C, with the veligers remaining benthic and metamorphosing immediately after hatching. Different modes of development have been previously reported for *C. nana* by Harris *et al.* (1975) who found planktotrophic development in 1971 and nonpelagic lecithotrophic development in 1973 in egg masses laid by individuals collected off the New Hampshire and Maine coasts. These differences may have resulted from observations on two virtually indistinguishable species, or *C. nana* may indeed possess two modes of development with the factors that influence the developmental pattern remaining enigmatic.

I wish to thank Larry G. Harris for his stimulation and guidance, Richard Strathmann and Alan Kohn for critically reading early drafts of the manuscript, and Alan Kuzirian for his friendly assistance. T. E. Thompson and Greg Brown kindly verified the identity of *Cuthona nana*. Carol Ann Kearns helped draw some of the figures. My wife, Mary-Jane, was a constant source of encouragement. The support of a University of New Hampshire Graduate Fellowship is gratefully acknowledged.

Summary

1. The larval development, metamorphosis, and postlarval growth of the eolid nudibranch, *Cuthona nana*, is described. Hatching occurred within 19 days at 11–13° C. The lecithotrophic veligers remained nonpelagic and proceeded to metamorphose within another two days.

2. Adult nutrition did not affect egg size or subsequent development and metamorphosis.

3. Embryogenesis, hatching, and metamorphosis were unaffected by the presence or absence of the adult nudibranch's prey, the hydroid *Hydractinia echinata*.

4. Different temperatures altered the rate of development and of metamorphosis but not the type of development. Egg masses collected in the field and incubated at the temperature at which they were collected invariably produced nonpelagic lecithotrophic veligers which then metamorphosed.

5. Newly metamorphosed specimens of *C. nana* survived for up to six weeks at 11–13° C and ten weeks at 4° C in the absence of *H. echinata*.

6. In the presence of abundant food, specimens of *C. nana* deposited fertile egg masses within 11 weeks after metamorphosis at 11–13° C, and continued feeding and ovipositing for two months.

7. *Cuthona nana* feeds specifically on *Hydractinia echinata*, which in Gosport Harbor is found predominantly on shells occupied by *Pagurus acadianus*. As the hermit crabs move about, postlarvae of *C. nana* are swept up by the gastrozooids of *H. echinata*, are not eaten by the polyps but reorient and feed on hydroid tissue.

8. Nonpelagic development in *C. nana* appears to result in a patchy distribution of postlarvae on the bottom, and an uneven, nonrandom distribution of young nudibranchs on the *H. echinata* colonies.

9. *Cuthona nana* does not kill the *H. echinata* colonies it preys upon, but only crops some of the polyps before leaving the colony to find a mate or deposit eggs. Lost polyps are subsequently regenerated.

LITERATURE CITED

Bayne, B. L., 1972. Some effects of stress in the adult on the larval development of *Mytilus edulis*. *Nature*, **237**: 459.

Bayne, B. L., P. A. Gabbott, and J. Widdows, 1975. Some effects of stress in the adult on the eggs and larvae of *Mytilus edulis* L. *J. Mar. Biol. Assoc. U.K.*, **55**: 675–689.

Berrill, N. J., 1931. The natural history of *Bulla hydatis* Linn. *J. Mar. Biol. Assoc. U.K.*, **17**: 567–571.

Bonar, D. B., 1976. Molluscan metamorphosis: a study in tissue transformation. *Am. Zool.*, **16**: 573–591.

Bonar, D. B., and M. G. Hadfield, 1974. Metamorphosis of the marine gastropod *Phestilla sibogae* Bergh (Nudibranchia: Aeolidacea) I. Light and electron microscopic analysis of larval and metamorphic stages. *J. Exp. Mar. Biol. Ecol.*, **16**: 227–255.

Bunting, M., 1894. The origin of sex-cells in *Hydractinia* and *Podocoryne;* and the development of *Hydractinia*. *J. Morphol.*, **9**: 203–236.

Casteel, D. B., 1904. The cell-lineage and early larval development of *Fiona marina*, a nudibranch mollusc. *Proc. Acad. Nat. Sci. Phila.*, **56**: 325–405.

Cazaux, C. 1961. Signification et origine de l'association entre Hydractinie et Pagure: rôle des tropismes larvaires dans le développement de l'hydraire. *Bull. Sta. Biol. Arcachon*, **13**: 1–5.

Christensen, H. E., 1967. Ecology of *Hydractinia echinata* (Fleming) (Hydroidea, Athecata) I. Feeding biology. *Ophelia*, **4**: 245–257.

Christensen, H. E., 1977. Feeding and reproduction in *Precuthona peachi* (Mollusca Nudibranchia). *Ophelia*, **16**: 131–142.

Farran, G. P., 1903. The nudibranchiate molluscs of Ballynakill and Bofin Harbours, Co. Galway. *Rept. Fish. Ireland for 1901*, pt. **2**: 123–132.

Franz, D. R., 1970. Possible variability in larval development between populations of the cephalaspid opisthobranch *Acteocina canaliculata*. *Am. Malacol. Union Inc. Bull.*, **37**: 68–69.

Franz, D. R., 1971. Development and metamorphosis of the gastropod *Acteocina canaliculata* (Say). *Trans. Am. Microsc. Soc.*, **90**: 174–182.

Gerlach, S. A., D. K. Ekström, and P. B. Eckardt, 1976. Filter feeding in the hermit crab, *Pagurus bernhardus*. *Oecologia*, **24**: 257–264.

Graham, J. J., 1970. Coastal currents of the western Gulf of Maine. *Int. Comm. Northwest Atl. Fish. Res. Bull.*, **7**: 19–31.

Grant, W. C., Jr., 1963. Notes of the ecology and behavior of the hermit crab, *Pagurus acadianus*. *Ecology*, **44**: 767–771.

Grant, W. C., Jr., and P. J. Pontier, 1973. Fitness in the hermit crab *Pagurus acadianus* with reference to *Hydractinia echinata*. *Bull. Mt. Desert Isl. Biol. Lab.*, **13**: 50–53.

Grant, W. C., Jr., and K. M. Ulmer, 1974. Shell selection and aggressive behavior in two sympatric species of hermit crabs. *Biol. Bull.*, **146**: 32–43.

Harris, L. G., L. W. Wright, and B. R. Rivest, 1975. Observations on the occurrence and biology of the acolid nudibranch *Cuthona nana* in New England waters. *Veliger*, **17**: 264–268.

Hendler, G., and D. R. Franz, 1971. Population dynamics and life history of *Crepidula convexa* (Gastropoda: Prosobranchia) in Delaware Bay. *Biol. Bull.*, **141**: 514–526.

Hyman, L. H., 1940. *The Invertebrates, Vol. I: Protozoa through Ctenophora.* McGraw-Hill Book Company, Inc., New York, 726 pp.

Jensen, K., 1970. The interaction between *Pagurus bernhardus* (L.) and *Hydractinia echinata* (Fleming). *Ophelia*, **8**: 135–144.

Jensen, K., 1975. The profit to *Pagurus bernhardus* (L.) by the presence of *Hydractinia echinata* (Fleming). *Biokon Rep.*, **1**: 1–4.

Loder, T., F. E. Anderson, and T. C. Shevenell, 1973. *Sea monitoring of emplaced baled solid waste.* University of New Hampshire Report, U.N.H. SG-118, 107 pp.

Orton, J. H., 1927. On the mode of feeding of the hermit crab, *Eupagarus bernhardus*, and some other Decapoda. *J. Mar. Biol. Assoc. U.K.*, **14**: 909–921.

Pelseneer, R., 1911. Reserches sur l'embryologie des gastropodes. *Acad. Roy. Belg. Cl. Sci. Mem. Collect. (Quarto)*, **3**: 1–167.

Rao, K. V., 1961. Development and life history of a nudibranchiate gastropod *Cuthona adyarensis* Rao. *J. Mar. Biol. Assoc. India*, **3**: 186–197.

Rasmussen, E., 1944. Faunistic and biological notes on marine invertebrates. I. The eggs and larvae of *Brachystomia rissoides* (Hanl.), *Eulimella nitidissima* (Mont.), *Retusa truncatula* (Brug.) and *Embletonia pallida* (A. & H.), (Gastropoda marina). *Vidensk. Medd. Dan. Naturhist. Foren.*, **107**: 207–233.

Rees, W. J., 1967. A brief survey of the symbiotic associations of Cnidaria with Mollusca. *Proc. Malacol. Soc. London*, **37**: 213–231.

Roginskaya, I. S., 1962. Reproductive biology and life cycle of *Cuthona pustulata* (Gastropoda, Nudibranchia). *Dokl. Akad. Nauk. SSSR Ser. Biol.*, **146**: 488–491.

Schijfsma, K., 1935. Observations on *Hydractinia echinata* (Flem.) and *Eupagurus bernhardus* (L.). *Arch. Neerl. Zool.*, **1**: 261–314.

Spight, T. M., 1975. Factors extending gastropod embryonic development and their selective cost. *Oecologia*, **21**: 1–16.

Sutherland, J. P., 1975. Life histories and the dynamics of fouling communities. Pages 137–153 in J. D. Costlow, Ed., *The ecology of fouling communities.* U.S.—U.S.S.R. Cooperative Program, Duke University Marine Laboratory, Beaufort, North Carolina.

Swennen, C., 1961. Data on distribution, reproduction and ecology of the nudibranchiate molluscs occurring in the Netherlands. *Neth. J. Sea Res.*, **1**: 191–240.

Tardy, J., 1970. Contribution a l'étude des métamorphoses chez les nudibranches. *Ann. Sci. Nat. Zool. Biol. Anim.*, **12**: 299–370.

Thompson, T. E., 1958. The natural history, embryology, larval biology and post-larval development of *Adlaria proxima* (A. & H.) (Gastropoda, Opisthobranchia). *Phil. Trans. Roy. Soc. Lond. Ser. B*, **242**: 1–58.

Thompson, T. E., 1962. Studies on the ontogeny of *Tritonia hombergi* Cuvier (Gastropoda Opisthobranchia). *Phil. Trans. Roy. Soc. Lond. Ser. B*, **245**: 171–218.

Thompson, T. E., 1967. Direct development in a nudibranch, *Cadlina laevis*, with a discussion of developmental processes in Opisthobranchia. *J. Mar. Biol. Assoc. U.K.*, **47**: 1–22.

Van de Vyver, G., 1964. Étude histologique du développement d'*Hydractinia echinata* (Flem.). *Cah. Biol. Mar.*, **5**: 295–310.

Van de Vyver, G., 1967. Étude du développement embryonnaire des hydraires athécates (gymnoblastiques) à gonophores. *Arch. Biol.*, **78**: 451–518.

Wobber, D. R., 1970. A report on the feeding of *Dendronotus iris* on the anthozoan *Cerianthus* sp. from Monterey Bay, California. *Veliger*, **12**: 383–387.